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Lower Devonian fishes from Saudi Arabia*

P.L. FOREY, V.T. YOUNG and H.A. McCLURE

Department of Palaeontology, Natural History Museum, Cromwell Road, London SW7 5BD

CONTENTS

Synopsis. Fragmentary fishes preserved in bone beds are described from the Jauf Formation and Wajid Sandstone of Saudi Arabia. They support previous opinions that the Jauf Formation represents a shallow and marginal marine deposit of Pragian age. Identification of a similar but more restricted fish fauna in the Wajid Sandstone suggests that at least part of this deposit, originally designated as 'Lower Permian and older?', should also be considered as Pragian. Two new taxa are described: *Wajidosteus minutus* gen. et sp. nov. is a small phlyctaeniid arthrodire and *Jaufolepis striata* gen. et sp. nov. is a new diplacanthid acanthodian. The fauna is compared with other Lower and Lower/Middle Devonian fish faunas. The Saudi fauna seems most similar to an Eifelian fauna from Khush Yeilagh, northern Iran, and is to be considered part of the Rhenish Bohemian faunal realm. Some notes are included on the sedimentology and palaeoenvironmental interpretation of the fish-bearing sediments.

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INTRODUCTION

Palaeozoic rocks in the Arabian Peninsula occur extensively in the sedimentary outcrop belt of central and western Saudi Arabia, wrapped around the Arabian Precambrian shield in a north–south trending arcuate band that covers a distance of over 1500 km. Sequences of more limited extent also occur in part of Oman. The Devonian rocks, while extensively distributed in the subsurface of eastern Arabia, are of limited geographical extent at the surface since they are usually truncated at Pre-Permian and Cretaceous erosion intervals. Outcrops of Devonian rocks occur in northwest Saudi Arabia in the Jawf/Sakakah area, where they are mapped in the successively younger Tawil Sandstone, Jauf, and Jubah (Sakaka) Sandstone formations, and at a recently discovered site located far to the south in the southernmost part of the Wajid Sandstone (Jibal al Wajid) complex (Fig. 1). Devonian fishes are found in both areas. An analysis of the Devonian rocks of Saudi Arabia is given by Boucot *et al.* (1989) and surface Devonian rocks are indicated on the maps of the United States Geological Survey (Bramkamp *et al.* 1963*a*, *b*) and on maps of the Saudi Arabian Ministry of Petroleum and Minerals (Meissner *et al.* 1986, 1989). Original description and definition of Devonian rock units are found in Powers *et al.* (1966) and Powers (1968). Boucot *et al.* (1989) presented a study of the palaeontology, biostratigraphy and biogeography of the Devonian of Saudi Arabia, which concentrated on the outcrop of the Jauf Formation. The basis for that study was fossils collected by one of us (H.A.M.) and others of the Arabian American Oil Company (now Saudi Aramco) in 1987–8.

The Devonian rocks containing the fishes are sandstones, shales and occasional limestones which were deposited on a broad, tectonically stable epicontinental shelf, the Arabian platform. Depositional environments of the Devonian range from continental to shallow marine. The Jauf Formation is approximately 300 m thick at the type locality and is composed of shale, limestones and minor sandstones, which together with the fossils suggest environments ranging from fluvial and flood plain to marine. The overlying Jubah Sandstone is largely continental. Marine transgressions and regressions caused by eustatic changes occur throughout the Jauf Formation (Fig. 2). The fossils from the Jauf Formation date this deposit as Pragian to early Emsian, while the underlying Tawil Sandstone is dated as early Devonian on the basis of brachiopods (Boucot *et al.*, 1989). The immediately overlying and conformable Jubah Sandstone is considered Emsian.

OCCURENCE OF FOSSIL FISHES AND PLANTS AND DEPOSITIONAL ENVIRONMENTS

Palaeozoic fishes from the Devonian of the Arabian Peninsula are very poorly known. Powers *et al.* (1966) listed dermal scutes of fishes as occurring in the Jauf Formation. Bahafzallah *et al.* (1981) mentioned the occurrence of fish remains in the Jauf. An arctolepid plate was described from a Devonian borehole sample from Qatar (White 1969). Turner (*in* Boucot *et al.* 1989) described acanthodian and placoderm scales from the Jauf Formation and Lelièvre (1989) described a head plate of a buchanosteid arthrodire. The fossil fishes described in this paper come from 12 selected sample localities: one in the Wajid Sandstone, nine in the Jauf Formation and two in the Jubah Sandstone. Other fish-bearing beds occur in the section but fossil specimens are rare or too badly preserved to warrant analysis.

Fish remains in the Jauf Formation and Jubah Sandstone appear to occur in three contexts which probably represent different depositional environments (Fig. 3). These are: (1) coarse to medium-grained and poorly sorted sandstone often with rip up clasts and channel features, probably of continental flood plain and fluvial nature where fish are most common and with no marine fossils (except very rare lingulids); (2) claystone, where the other fossils associated with the fishes are mostly small lingulids, an environment which possibly represents deposition in mud lagoons with very brackish water, or perhaps estuarine ponds; (3) limestones containing brachiopods, trilobites, corals and molluscs and which represent shallow water marine conditions in which fish fossils are very rare.

The depositional environments of the Jauf Formation are discussed in more detail in Boucot *et al.* (1989) and the probable specific environments of each of the samples studied in this paper are given in the Appendix (p. 41). A remarkable feature of the formation is the rapid and extremely brief sea-level fluctuations recorded in the section (Fig. 2).

Fossil fishes and plants from the Wajid Sandstone occur in very silty, well indurated, varicoloured micaceous claystone with indistinct irregular bedding and discrete 'floating' fine sand grains. Of limited geographic extent and only 1.5 m thick, the unit either lies directly on basement complex, or is unconformably separated from the basement by a thin, well sorted, medium grained sandstone. This basal sandstone, where present, varies rapidly in thickness but is uniform in texture and mineral content. This suggests that it developed as a discontinuous deposit marginal to a large water body and that it probably infilled local topographic lows in the basement terrain. The excellent sorting and low angle to planar crossbedding suggests that it was not of fluvial origin. A low energy, quiet water environment is indicated by the claystone containing the fishes and the discretely scattered sand grains may indicate transportation by wind. Frequent small clusters and string-like occurrences of sand grains may be faecal in origin. The claystone is overlain by a distinct desiccation horizon and then partly by a geographically extensive sandstone which is thick, coarse-grained, and massively bedded with some cross bedding. This is the more typical Wajid Sandstone facies which probably represents deposition in extensive flood plain and fluvial environments. The fish- and plantbearing claystone is interpreted as having been deposited in a highly restricted quiet water basin, possibly a cut off lagoon (or perhaps a lake). No other fossils are present to aid interpretation of the environment. The underlying sandstone may represent a shoreline facies, where both aqueous and aeolian processes enhanced the sediment maturity. Eventually the basin filled in and severe desiccation followed, prior to the final inundation by coarse, fluvially-transported sands of the massive Wajid Sandstone. The claystone unit was not previously recognized and so no fossils were thought to occur in the Wajid Formation; hence the previous dating as 'Lower Permian and older' (Powers *et al.* 1966 ; Powers 1968). The contained Devonian fishes described in this paper suggest that at least the basal claystone unit is Devonian and

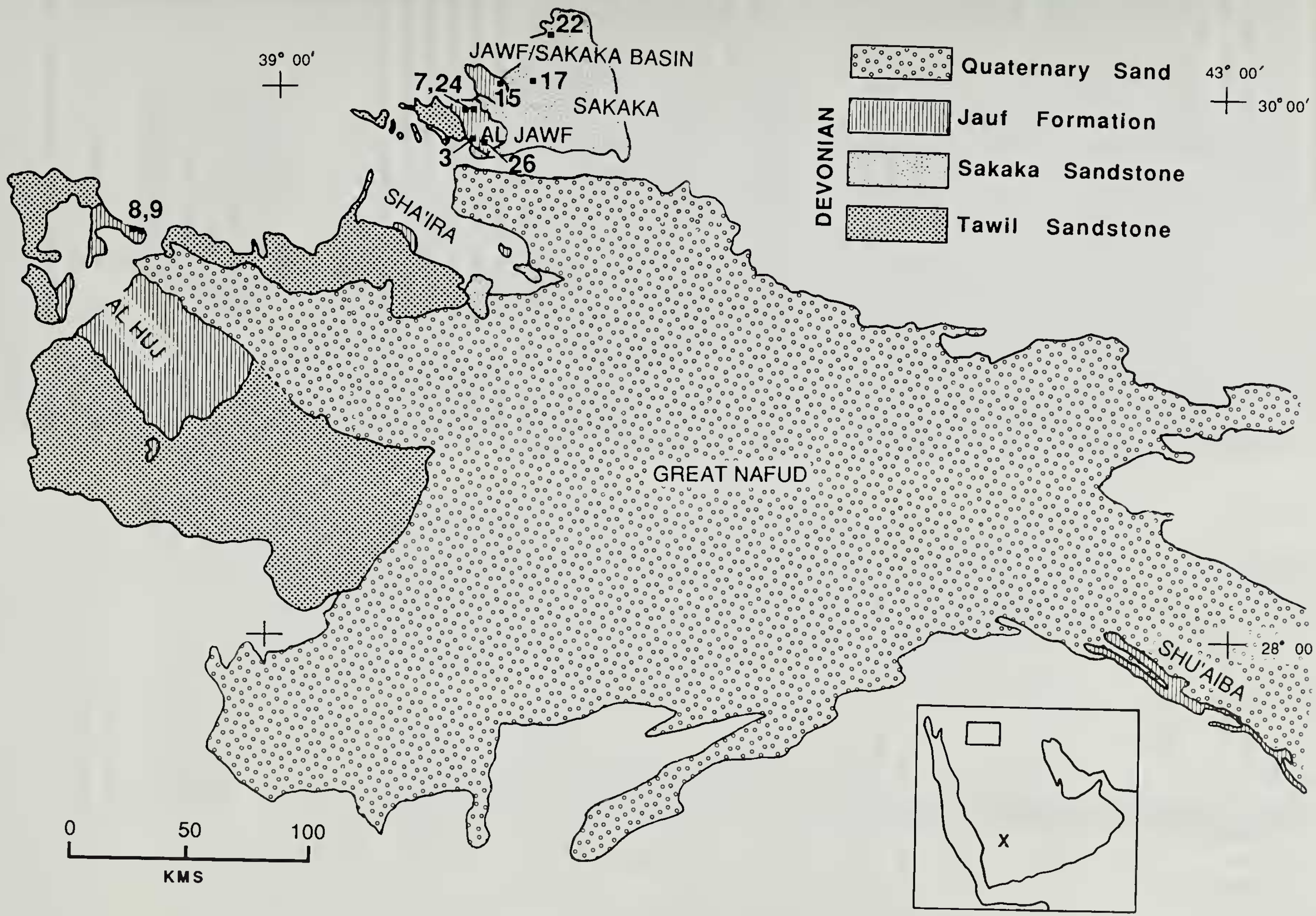


Fig. 1 Map showing the Devonian outcrop area in Saudi Arabia. The localities in the Jauf Formation are numbered to correspond with those used throughout this paper. The Wajid Sandstone locality in the south of the country is shown only in the inset map, indicated by **X**. The Wajid Sandstone is part of a sequence as yet unmapped. [Modified after Boucot *et al.* 1989.]

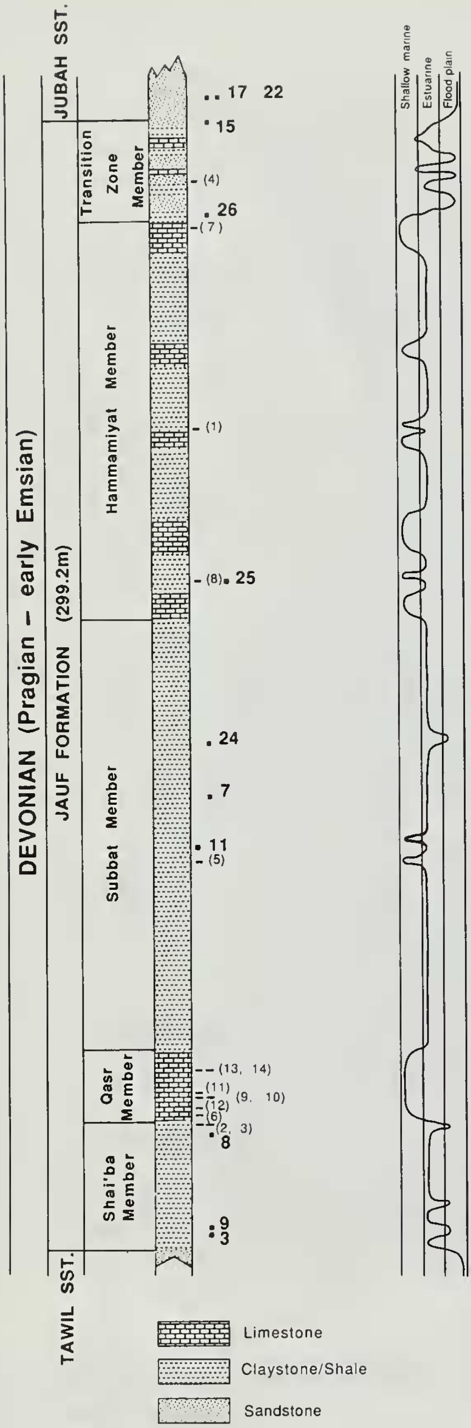


Fig. 2 Generalized stratigraphic section of the Jauf Formation. The lithologies shown are general; for detailed descriptions of the sampled parts of the section see the Appendix. The position of the sample numbers are shown with those examined and numbered by Boucot *et al.* (1989) given in parentheses. On the whole Boucot *et al.* sampled the more truly marine levels. The transgressive/regressive curve to the right is based upon evaluation of several parameters: lithology, fossil content from all available samples, lithology/fossil associations, fossil/fossil associations, and sedimentary features.

contemporaneous with the Subbat Shale Member of the Jauf Formation. The few small plant fragments in the Wajid cannot be usefully identified.

The Jubah Sandstone (see Meissner *et al.*, 1989 for definition) is largely of continental origin. The only fossil known, except for the fishes described here, is a herbaceous lycophyte similar to *Haskinsia* or *Colpodexylon*, which occur in Middle and Upper Devonian rocks in Laurentia. While most of the Jubah Sandstone may be considered continental in origin, the occurrence of a single lingulid brachiopod together with the fishes in Sample 22 (see Appendix, p. 42) may serve to indicate a very brief marginal marine or estuarine phase near the base of the sequence. The other Sample (17, p. 42) appears to represent a shallow stream deposit, perhaps laid down in a braided flood plain. The overall sedimentary evidence and fossil associations documented (stream or flood plain or outwash deposits) probably indicates a fresh-water aspect to most of the fish beds studied here, although there was possibly some brackish water incursions due to backflooding in an estuarine situation. Sample 22 (p. 42) contains only one lingulid specimen in what otherwise appears to be fluvial outwash deposit, which might mean that the marine back flooding was only due to an exceptional storm tide.

SYSTEMATIC PALAEONTOLOGY

In this section the fishes from both the Jauf Formation and the Wajid Sandstone are described. Some taxa are common to both. In many cases the specimens are broken, meaning that photographs are less useful than the drawings which combine information from more than one specimen. Where sample numbers are given these refer to those cited in the Appendix and plotted on the section (Fig. 2). All specimens referred to by register number are in the collections of the Department of Palaeontology, Natural History Museum.

Abbreviations. The following abbreviations are used in the descriptions of the fishes: ADL, anterior dorso-lateral plate; AMV, anterior medio-ventral plate; AL, anterior lateral plate; AV; antero-ventral plate; AVL anterior ventro-lateral plate; IL, intero-lateral plate; MD, median dorsal plate; PDL posterior dorso-lateral plate; PMV, posterior medio-ventral plate; SP, spinal plate.

Subclass **PLACODERMI**
Order **ARTHRODIRA**
Suborder **PHLYCTAENOIDEI**
Infraorder **PHLYCTAENII**
Phlyctaenii incertae sedis

Genus ***WAJIDOSTEUS*** nov.

Diagnosis. Very small phlyctaenioid arthrodire measuring an estimated 14 mm across the ventral trunk shield at the level of the interolaterals. The ventral shield is longer than wide. Spinals are stout, reaching just beyond the posterior level of the AVL and bearing about 20 small medial denticles. Trunk shield tall, with both AL and ADL being deeper than long. ADL with small trochlear. Overlap surface on ADL for the MD (unknown) is sinuous. Ornament consists of many fine tubercles, regularly spaced.

NAME. After the Wajid Sandstone, the formation in which the holotype was found.

Wajidosteus minutus **sp. nov.** Figs 4, 5, 21, 22

DIAGNOSIS. As for genus, only species.

HOLOTYPE. P62836a, b ADL in part and counterpart, Wajid Sandstone, 17°36′N 44°5.5′E.

MATERIAL. P62826 (AL), P62827 (left AVL, SP), P62828 (left IL, SP, AVL), P62829 (left AVL, SP), P62830 (crushed trunk shield with a few trunk scales), P62831 (left IL, SP, AVL), P62832 (left AVL, SP), P62833a, b (AL), P62834a, b (right IL, SP+AVL), P62835a, b (AL): all from Wajid Sandstone. Specimen P62865 from sample 3, Jauf Formation, is the impression of an AVL.

DESCRIPTION. This species is known only from a few isolated trunk plates and a badly crushed shield with scales. Association of individual plates is suggested by the similarity in ornament and congruent size. Even though the specimens are very small it is probable that they represent adult growth stages because the sutures between IL, SP and AVL are obscured and these elements tend to hold together in the few available specimens. Using the synapomorphy scheme proposed by Goujet (1984) *Wajidosteus* is recognized as a phlyctaenioid by the presence of a trochlear, implying a ball and socket neck joint, and the absence of an AV plate (synapomorphy of actinolepidoids). It is suggested that it is a phlyctaeniid because the spinal plates are relatively strongly developed but, within this assemblage of about 15 genera, comparisons become imprecise. One unusual feature of *Wajidosteus* is that both the AL and ADL are restored as being deep (Fig. 5). Amongst phlyctaeniids this is seen in the monotypic forms such as *Tiaraspis* Gross 1962, *Kolpaspis* Pageau 1969, *Gaspeaspis* Pageau 1969 and *Aggeraspis* Gross 1962. The overall size of this placoderm is most like that of *Huginaspis* or *Gaspeaspis*, as is the posterodorsal process upon the AL (Pageau 1969: pl. 33, fig. 7B). The ADL is the most distinctive of the known elements and a specimen of this is chosen as the holotype. It resembles that of *Tiaraspis* in that the dorsal overlap surface is sigmoidal (in most phlyctaeniids it is straight). The lateral line is deeply incised along the middle of the ADL and there is an accessory twig of the lateral line. However, unlike *Tiaraspis* and *Groenlandaspis* Heintz 1932 there is no evidence that the ADL's of either side met one another beneath the MD (unknown in *Wajidosteus*). The AMV is badly preserved in specimen P62828 but it seems to be short and broad and triangular implying that there was little or no contact with the PMV. The ornament is developed as tiny tubercles, regularly arranged and distributed evenly; it becomes coarser at the level of the trochlear on the ADL and along the outer margin of the spinal. In all, the shape of the trunk shield and the ornament most closely resembles that illustrated for *Huginaspis* by Heintz (1929: pl. 3), differing mainly in the slightly longer spinals and the presence of an accessory twig of the lateral line.

cf. ***Elegantaspis*** Heintz 1929 Fig. 6

The present collection contains one specimen from the Wajid Sandstone (P62837: a trunk shield, parts of head plates and a few scales). Virtually no detail may be seen and comparisons with other placoderms can only be on the most superficial level and is restricted to overall shape. This specimen is considered to be a phlyctaeniid because of the long narrow trunk shield and the long spinal. Like *Wajidosteus* it is a very small placoderm, the trunk shield measures 22 mm long. The spinal is long; although incomplete it was probably longer than the trunk shield, and is straight without medial tubercles. These features are very similar to those of *Elegantaspis recticornis*, a species described from the Siegenian Wood Bay Series of Spitzbergen (Heintz 1929).

Order **PETALICHTHYIDA**

Gen. et sp. indet. Fig. 23

Several specimens within samples 3 and 11, Jauf Formation, may be compared to petalichthyid placoderms but the comparison is based mainly on similarities in the pattern of ornamentation and identification must remain tentative until more complete specimens are found. Specimen P62863a, b appears to be part of a head shield and, to judge from the patterns of ornament, there are parts of three plates represented. It is not possible to identify the plates. The ornament consists of smooth tubercles which are arranged in groups of two, three or four at the presumed centre of ossification and then they are arranged in radiating rows towards the margins of the plates. P62949 (sample 11) is an ADL showing well the prominent lateral line developed as a series of pores. Specimens P62862, P62950 (sample 11) and P62863a, b show small portions of spinal plates with similar ornament. In these spinals the tubercles of ornament are aligned along about seven clearly defined rows. The tubercles are closely spaced and are of constant size, and are slightly flattened from side to side and also slightly asymmetrical so that the tips tilt towards the distal end. The leading edge of the spinal is ornamented with slightly enlarged tubercles while the trailing edge bears prominent denticles angled towards the base of the spinal. This type of ornament is identical to that found in petalichthyids, and of all petalichthyids the Saudi specimens resemble *Wijdeaspis* most closely. This is a genus with species found in the Eifelian of Spitzbergen (*W. arctica* (Heintz 1929)), Emsian of New South Wales (*W. waroonensis* Young 1978) and Eifelian of Severnaya Zemlya , Taimyr and the Siberian platform (*Wijdeaspis* sp. (Obruchev 1967)). From the Wajid Sandstone there is a single specimen (P62838) representing a nuchal plate probably referable to a petalichthyid. The plate is very elongate and each lateral margin is embayed as three shallow excavations marking the contact edges with anterior and posterior paranuchals, centrals and preorbitals. The shape of this nuchal matches that seen in petalichthyids such as *Wijdeaspis*, *Notopetalichthys* (Emsian of New South Wales), *Shearsbeaspis* (Emsian of New South Wales) and *Lunaspis* (Siegenian–Emsian of Germany, Emsian of New South Wales and the Lower Devonian of China).

Other placoderms

Amongst the collection from the Wajid Sandstone there are several specimens of larger placoderms which cannot be associated with each other, nor can they be closely identified. Two of these can reasonably be phlyctaeniids. P62843 is a long shallow PDL, 30 mm long and 10 mm high; it is rectangular, very similar in shape to that figured for *Dicksonosteus*

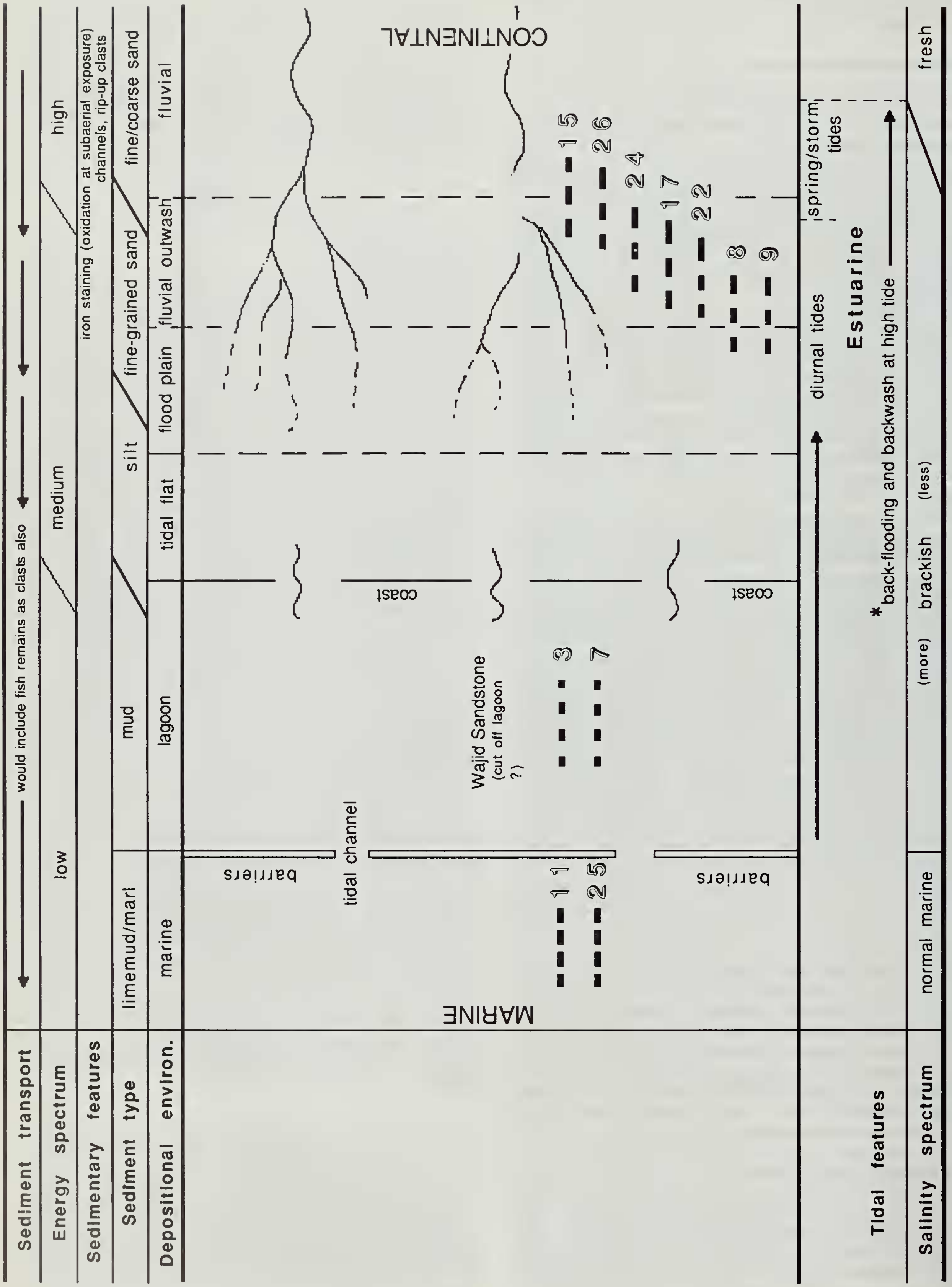
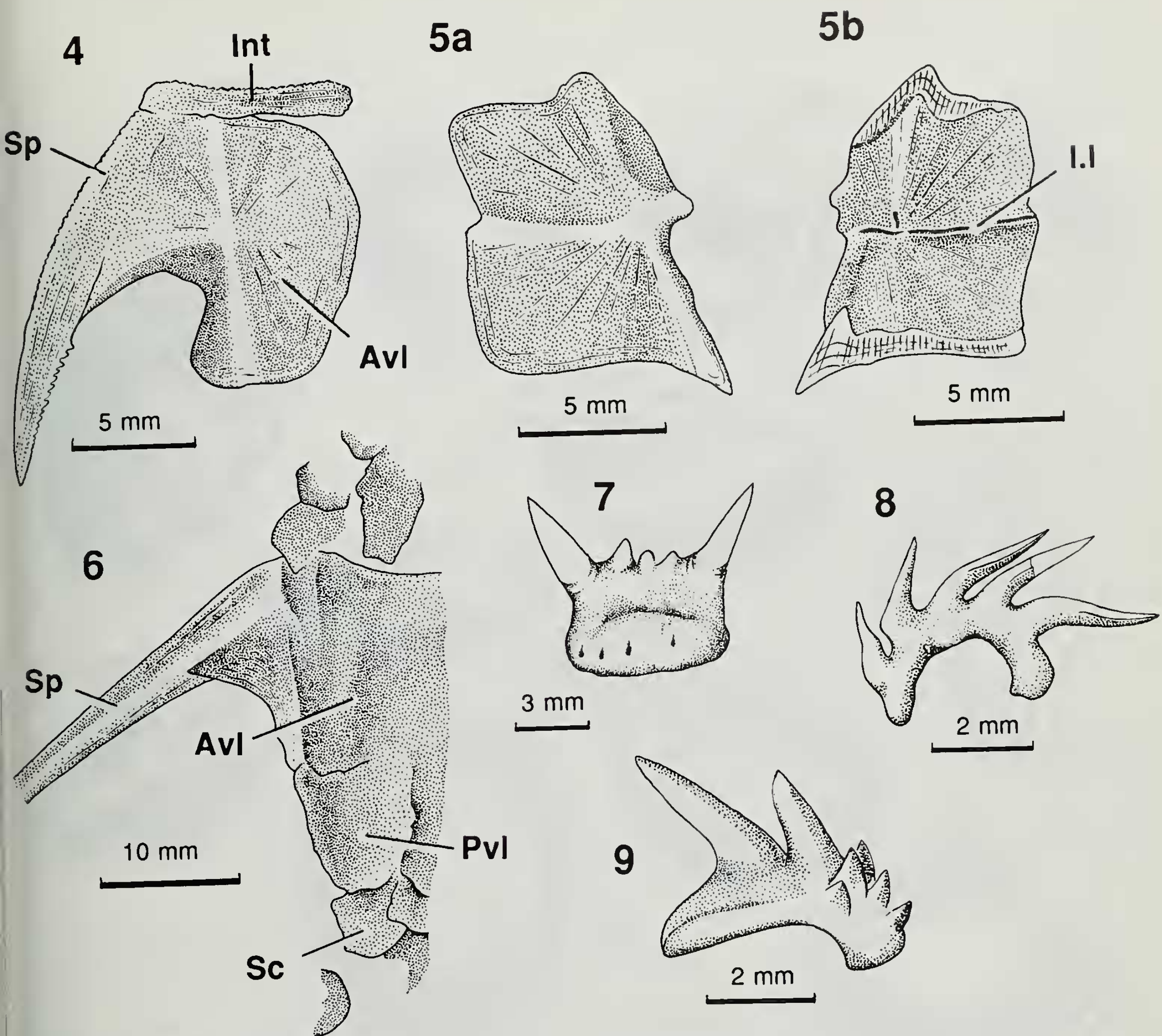


Fig. 3 Environmental and sedimentological scenario of the fish-bearing localities in the Jauf Formation and Wajid Sandstone, based on sedimentological and palaeontological evidence.



Figs 4–5 *Wajidosteus minutus* gen. et sp. nov. 4, ventral view of part of ventral trunk armour, based on P62831. Sp – spinal, Int – intero-lateral, Avl – anterior ventrolateral. 5, Anterior dorso-lateral ; a inner, b outer views. **Holotype** P62836a, b. l.l – lateral line groove. (See also Fig. 22).

Fig. 6 cf. *Elegantaspis*. Ventral trunk armour, scattered head plate and scales. P62837. Sp – spinal, Avl – anterior ventro-lateral, Pvl – posterior ventrolateral, Sc – scale.

Fig. 7 *Phoebodus* sp. tooth P62874, tips of lateral cusps restored.

Fig. 8 Ischnacanthid symphysial tooth whorl. P62867.

Fig. 9 cf. *Onychodus anglicus* Woodward. Tooth whorl. P62853.

›y Goujet (1984: fig. 63). Others (P62839 and P62840) are \Ls, 18 mm and 22 mm deep but otherwise similar in shape o those of *Wajidosteus*. Two further specimens are long, offin-shaped AMVs (P62842, P62846a, b), much narrower han those seen in *Wajidosteus*. P62845a, b and P62848 are imilar shaped AVL plates, 22 mm and 34 mm long respecively and the spinal margin shows that the placoderm to vhich they belonged had very divergent spinals. P62841 is lso an AVL showing a divergent spinal margin but it is lightly more elongate. Lelièvre (1989) described the central late of a buchanosteid arthrodire from the Jauf Formation. 'here are plates with buchanosteid type ornament pattern in the present collection although we have been unable to identify them further.

Turner (*in* Boucot *et al.* 1989) recorded the occurrence of placoderm scales within a sample from the Jauf Formation and compared them with those of *Stensioella*. We have recovered more such scales from sample number 17 (P62958–60) and they are illustrated in Figs 16–18. Generally the scales are small, conical with a rough uneven surface of ridges, depressions and sometimes tubercles. The lower surface is deeply concave. Some are similar to those identified by Turner, others resemble scales attributed to *Asterosteus*, an

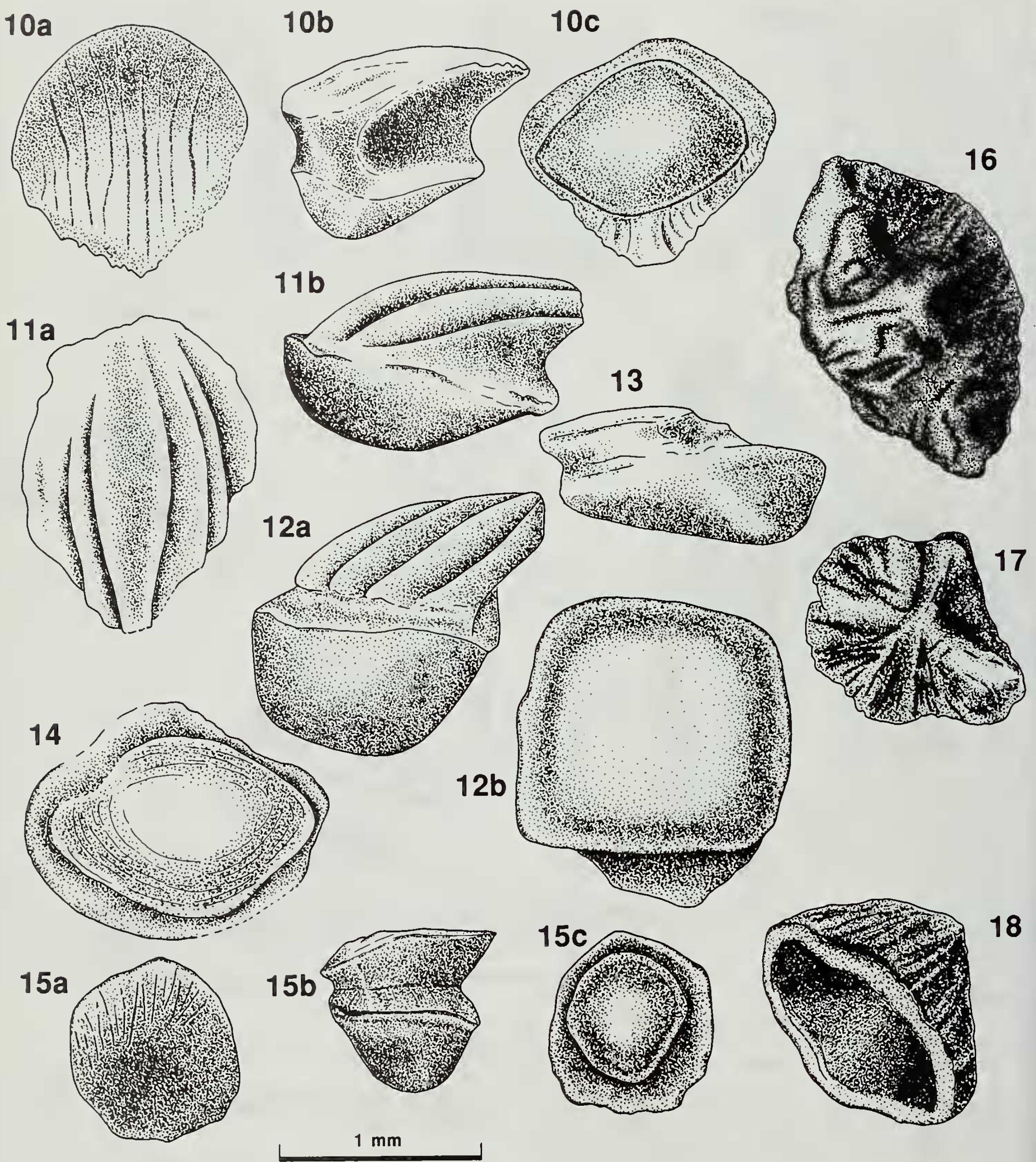


Fig. 10 Diplacanthid scale. a crown, b lateral, c basal views. P62951.

Fig. 11–14 *Nostolepis striata* Pander. 11, scale; a crown, b lateral views. P62954. 12, scale; a lateral, b basal views. P62952. 13, scale, lateral view. P62956. 14, scale, basal view. P62955.

Fig. 15 *Cheiracanthoides* cf. *comptus* Wells. Scale; a crown, b lateral, c basal views. P62953.

Figs 16–18 Three types of placoderms scales. 16, crown view P62958. 17, crown view P62959. 18, basal view P62960.

All figures to same scale. Scale bar applies to all.

Upper Devonian rhenanid (cf. Denison 1978: fig. 13).

Subclass **ACANTHODII**

The acanthodians are represented mostly as disarticulated scales and spines and this is not uncommon in many other Lower Devonian localities. The state of acanthodian taxonomy reflects this and many taxa are erected for either scales or spines. Because of this the scales are here treated separately from the spines.

Order **CLIMATIIDA**
Family **CLIMATIIDAE** Berg 1940 [scales]

Genus ***NOSTOLEPIS*** Pander 1856

Nostolepis striata Pander 1856 — Figs 11–14

MATERIAL. Scales from the Jauf Formation samples 3, 9, 17 (P62956), 22, 15 (P62954), 26 (P62952).

REMARKS. These scales have a deep, narrow crown which overhangs the base posteriorly, and is produced to a point. The neck is rhombic and hardly distinct as it passes from the crown into a deep, strongly convex base which often shows growth lines. The degree of convexity varies from scale to scale, and may reflect different growth stages and/or different sites of origin over the body. The surface ornament consists of several paired, pronounced, symmetrically arranged ridges, the central pair bordering a median boatshaped depression and converging posteriorly to form a point. The overall shape and histology of these scales are similar to those of climatiid scales. In that they have posteriorly converging ridges these scales are similar to *Nostolepis striata* as described by Wang & Dong (1989), *N. sinica* Gagnier, Janke & Shi 1989*a* and *N. costata* Goujet 1976, and to scales described by Giffin (1980) as *Cheiracanthoides comptus*. They differ from *N. sinica* in lacking serrated edges, and from Giffin's scales in lacking a median ornament ridge in the crown. Scales of *N. costata* were identified by Turner (*in* Boucot *et al.* 1989) from the Jauf Formation. The scales described here show the ornament ridges set at an angle, facing laterally, and in this respect they are most similar to scales described as *N. striata* by Wang & Dong (1989) and by Gross (1947). *N. striata* is elsewhere discussed by Novitskaya & Obruchev (1967) and by Pander (1856).

Cheiracanthoides cf. ***comptus*** Wells 1944 — Figs 15 a–c

MATERIAL. Scales from samples 22 (P62955), 15 (P62953), Jauf Formation.

REMARKS. Turner (*in* Boucot *et al.* 1989) had identified scales of *Cheiracanthoides comptus* within the Jauf Formation. Each of the scales we have identified shows a crown which is relatively flat-topped with only a slight bevel along the curved anterior margin. The gently curved anterior and posterior margins of the crown barely overhang the base, from which it is separated by a narrow and deeply incised neck. The base is deep, convex and shows obvious growth lines. The ornament consists of wide, shallow ridges irregularly arranged and separated by narrow grooves. The ridges converge slightly posteriorly where they become indistinct and therefore do not cover the entire crown. These scales are very similar to the *Cheiracanthoides comptus* scales described by Wells (1944: fig. 4a–c).

Family **DIPLACANTHIDAE** Woodward 1891

Gen. et sp. indet. — Fig. 10

MATERIAL. Scales from the Jauf Formation, samples 17, 22, 15, 26 (P62951). The crown is almost flat topped to gently convex. The anterior margin of the crown is curved in an arc. Low ridges run longitudinally from the anterior to the posterior margins of the crown, and are almost parallel to each other, diverging slightly anterolaterally. Posteriorly the margins of the crown converge to form a medial point. Posterolaterally the margins of the crown are sculptured to form an irregularly serrated margin. The posterior margin of the crown extends beyond the margin of the base, and the base is not visible from above in plan view. The anterior margins of the crown and base are approximately level. The neck is wide and forms a distinct division between the crown and the base. Towards the anterior the base is convex and quite deep. Its surface often shows parallel horizontal growth lines. The scales of this type from Saudi Arabia show a strong resemblance to scales of Givetian age from Antarctica (G.C. Young, personal communication and 1989: fig. 4C).

Genus ***JAUFOLEPIS*** nov.

DIAGNOSIS. Based on a patch of scales showing shallow bases and crowns of two sorts. Smaller scales have closely serrated posterior margins and a crown marked by faint longitudinal ridges towards the posterior margin. Larger scales have large, elongate crowns extending well beyond the base and ornamented with irregular ridges curving inwards posteriorly and becoming indistinct.

NAME. After the Jauf Formation.

Jaufolepis striata gen. et sp. nov. — Figs 19, 24

DIAGNOSIS. As for genus, the only species.

HOLOTYPE. P62957a, b, impressions of two kinds of scales from sample 24, Jauf Formation.

DESCRIPTION. The patch of scales contains two kinds of scale which very clearly belong to the same fish and no doubt grade into one another. Since only the bases of most of the scales are exposed it is not possible to determine the extent of this gradation. All the bases are shallow. Scales of the smaller type have a gently convex crown which extends posteriorly beyond the base. The posterior margins of the crown are serrated and the evidence of former growth stages is present as a delicate scalloped patterning. The surface of the crown is marked by faint longitudinal ridges towards the posterior margin. The anterior part of the crown was not seen. The larger scales have large, elongate crowns which extend a considerable way beyond the base. The surface is ornamented with faint ridges which curve inwards posteriorly to become indistinct. The posterior margin of the large scales is generally not well preserved but seems to taper to a point. The posterior outline seems to vary among scales but this may be an artifact.

The marked variation in scale types seen in P62957a, b is

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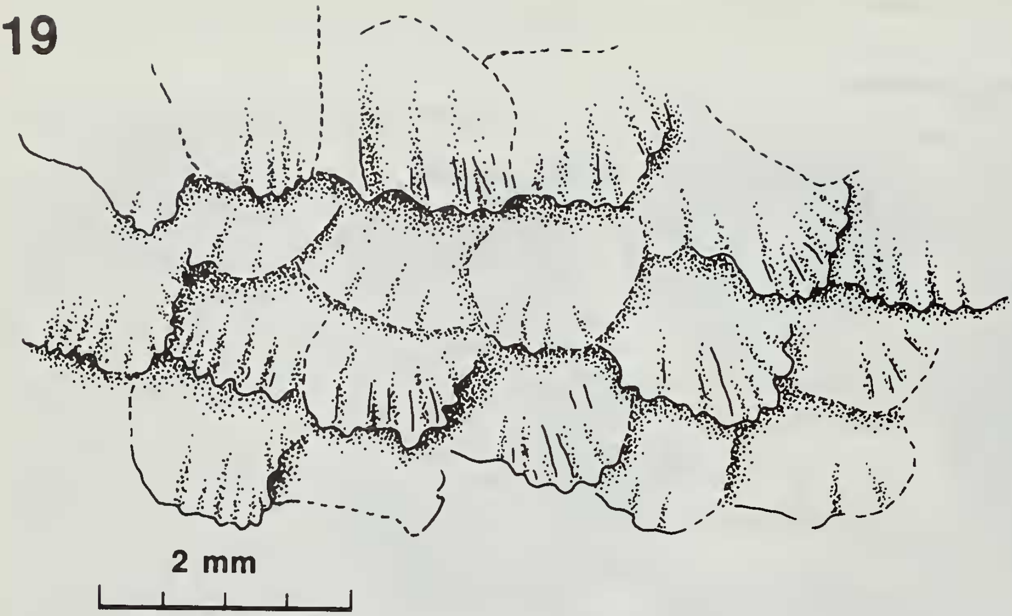

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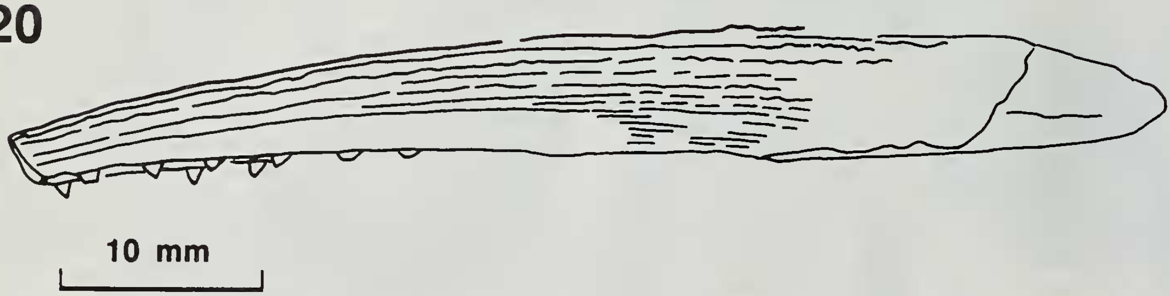


Fig. 19 *Jaufolepis striata* gen. et sp. nov. Group of small scales. **Holotype** P62957b. (See also Fig. 24).
Fig. 20 *Parexus* sp. Spine showing typical alternating arrangement of posterior denticles. P62870. (See also Fig. 25).

not seen in many other acanthodians. It is associated with the Diplacanthidae by virtue of the scalloped patterning within the crown and the surface ornament of longitudinal ridges, although the ridges are indistinct on the smaller scales.

Family **CLIMATIIDAE** Berg 1940 [spines]

Genus *Parexus* Agassiz 1845

Parexus sp. Figs 20, 25

MATERIAL. One almost complete spine, P62870 from sample 8.

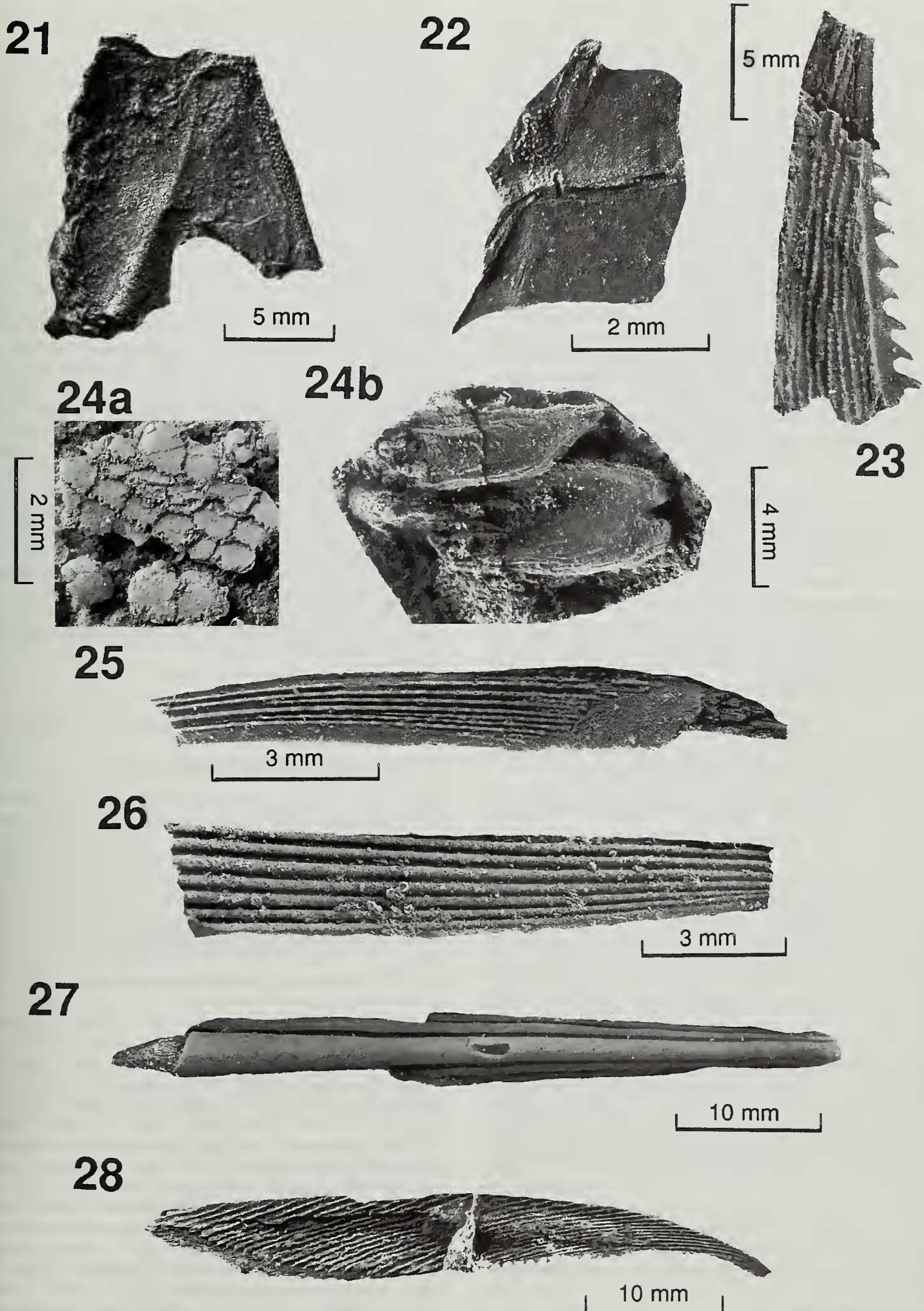
REMARKS. This is a slender spine with long narrow ridges running parallel to the axis and a short insertion area. Basally there are eight ridges but some fade out so that there are only four at the tip. The proximal ends of the ridges bear noded ornament. The spine is gently curved and slightly flattened from side to side; this latter feature is unlike the straight spines of *Parexus*. However, as in species of *Parexus* there are denticles arranged in alternate fashion at the distal end of the trailing edge.

Climatiidae *incertae sedis*

MATERIAL. Two fin spines P62857 and P62858. Both specimens are from sample 9 from the Jauf Formation.

Specimen P62858 is a portion, 62 mm in length, of a fin

Figs 21–22 *Wajidosteus minutus* gen. et sp. nov. 21, ventral view of part of ventral trunk armour. P62828 (cast). 22, ADL, cast of outer view. **Holotype** P62836b. (See also Fig. 5).
Fig. 23 Petalichthyid spine, Gen. et sp. indet. P62862.
Fig. 24 *Jaufolepis striata* gen. et sp. nov. a, group of small scales. b, two of the larger scales. **Holotype** P62957a, b.
Fig. 25 *Parexus* sp. Spine P62870 (cast). (See also Fig. 20).
Figs 26–27 *Uraniacanthus spinosus* Miles. 26, P62861 (cast). 27, spine P62860 (cast).
Fig. 28 cf. *Gyracanthus incurvus* Traquair. Spine P62814a (cast).


21
5 mm
22
2 mm
5 mm
23
24a
2 mm
24b
4 mm
25
3 mm
26
3 mm
27
10 mm
28
10 mm

spine. The spine is straight with strongly defined ridges running parallel to the axis of the spine. The ridges are of varying thicknesses, and are arranged in an irregular manner. Sometimes adjacent ridges merge to form a single ridge distally. Some of the ridges show a faint overlapping, ribbed ornament, similar to that of many climatiid spines, and these ornament nodes are aligned slightly obliquely to the ridges and to the spine. P62857 is 73 mm in length, and is preserved as an impression with some of the bony tissue still remaining. The spine is slender and is almost straight, with a very slight curvature. About 8 or 9 strongly defined ridges run parallel to the axis of the spine, and are ornamented with faint ribs which run obliquely outwards from the proximal end of the spine and towards the posterior margin of the spine. These features are most similar to the anterior dorsal spine of *Parexus*. However, unlike *Parexus* the posterior margin of spine number P62857 is strongly ribbed with oblique, closely spaced ribs which are orientated posterodistally. No posterior denticles are evident along the posterior margin of spine number P62857 as they are in *Parexus*. Thus while specimen number P62857 has similarities to *Parexus* and may be closely related,it does not seem to be a species of this genus.

Order **ISCHNACANTHIDA**
Family **ISCHNACANTHIDAE** Woodward 1891

Genus ***URANIACANTHUS*** Miles 1973 [spines]

Uraniacanthus spinosus Miles 1973 Figs 26, 27

MATERIAL. Two fin spines, P62860 and P62861, each preserved as impressions, and each incomplete. Both are from sample 9, Jauf Formation.

REMARKS. Latex rubber casts were prepared from the natural moulds. The remaining portion of P62860 is 41 mm in length, and for P62861 is 26 mm in length. The spines differ, and resemble different fin spines of this taxon.

Specimen P62860 is slender, elongate and straight with smooth, unornamented longitudinal ridges. A relatively wide, convex ridge forms the anterior margin of the spine, and on each side are deep grooves and two or three well defined and quite broad ridges. The ridges or grooves are parallel to the length of the spine and do not merge along the portion of the spine which is preserved. This spine has several similarities to *Devononchus* and to the posterior dorsal and pelvic spines of *Uraniacanthus spinosus*. In all of these the spines are slender, straight or nearly so, and have a wide convex longitudinal ridge along the anterior margin. On each side there are several strongly defined ridges and grooves, which run parallel to the axis of the spine, and which are smooth and unornamented. The spine from Saudi Arabia (P62860) has three ridges on each side of the anterior ridge. Five ridges are present on each side of *Devononchus*, and on the posterior dorsal and pelvic spines of *U. spinosus* two ridges are present. *Devononchus* is considerably larger than specimen P62860, the spines of *U. spinosus* are more comparable in size. The insertion area of *Devononchus* is relatively significantly longer than that of specimen P62860. Thus, specimen P62860 is more closely comparable to the posterior dorsal and pelvic fin spines of *U. spinosus* from the Lower Devonian (Upper Gedinnian), Dittonian, of Herefordshire (Miles 1973).

Specimen P62861 is very gently curved, and has seven strongly pronounced, smooth, unornamented, narrow ridges, parallel to each other and to the axis of the spine. The ridges remain separate and do not merge along the portion of spine preserved. An impression of a small portion of the anterior margin of specimen P62861 is preserved, and its shape suggests that the spine is somewhat flattened in section, laterally or dorsoventrally. Specimen P62861 is very similar to the pectoral or anterior dorsal spine of *U. spinosus*.

Gen. et sp. indet. [tooth whorls] Figs 8, 9

MATERIAL. Specimens P62866, P62867 from sample 3 represent symphysial tooth whorls. P62867 is the best preserved (Fig. 8) and shows five teeth, the longest of which is 2·8 mm long. Each tooth is monocuspid, and is sharply angled so that the point is directed away from the adjacent tooth. The teeth each form a sharp point at the tip and the upper part of the tooth has a slight lateral ridge but is otherwise smooth (cf. the striated teeth of *Onychodus*). The tooth whorl seems to be a median structure and is typical of tooth whorls described for members of the Ischnacanthidae. The Ischnacanthidae range from Upper Silurian (Ludlovian) to Upper Carboniferous (Westphalian B) from North America, Spitsbergen, Europe, Siberia and Iran (see Denison, 1979).

Specimen P62853 (Fig. 9), sample 9, contains a small fragment of a symphysial tooth whorl. The hollow base is swollen and there are the bases of at least six teeth preserved. It looks very similar to small tooth whorls found in the Downtonian of the Old Red Sandstone of the Anglo-Welsh basin and described as *Onychodus anglicus* Woodward 1888. These whorls are almost certainly those of climatiid acanthodians probably more correctly referred to the genus *Gomphonchus*.

Family **GYRACANTHIDAE** Woodward 1906 [spines]

cf. ***Gyracanthus incurvus*** Traquair 1890 Fig. 28

MATERIAL. Seven specimens, all from the Wajid Sandstone, represent acanthodian spines which have a characteristic ornament comparable to that in *Gyracanthus incurvus*.

REMARKS. The largest and best preserved of the spines (P62814a, b) is 52 mm long. P62816a, b is 16·5 mm long: P62811 and P62813a, b are an estimated 50 mm and 43 mm in length respectively, while the remaining three specimens P62812, P62810 and P62815a, b are fragments of spines only. The three more complete specimens show this spine to have a broad, shallow base of insertion as in spines of climatiids in general. They are gently curved, this curvature becoming more marked at the distal end, and the spine is ornamented with prominent ridges. The ridges on either side run obliquely across the spine and intersect one another in a chevron pattern along the leading edge. There are 20–22 ridges at the base of the spine, which is 17 mm wide in P62814a, b. Although the ridges appear smooth distally they are faintly nodose at their bases. The largest spine carries about 25 recurved denticles along the posterior edge.

These spines are comparable with those of *Vernicomacanthus* and *Gyracanthus* in that the ornament consists of ridges which intersect the leading edge and are faintly nodose, particularly at the base. The two recognized species of *Vernicomacanthus* are smaller than the Saudi specimens and the ridges, of which there are far fewer, are more strongly nodose. The Saudi spines are more comparable in size with *Gyracanthus incurvus* and there are about the same number of ridges which tend to be smooth except at the base. *G. incurvus* also has a series of posterior denticles, although there appear to be far fewer in the Saudi specimens. *G. incurvus* comes from the Lower/Middle Devonian of Campbellton, New Brunswick (Woodward 1892). Blieck *et al.* (1980: fig. 7) described spines from the Eifelian of Iran which look very similar to those described here, except that there do not seem to be any posterior denticles. This may be a preservational artefact.

Other acanthodians [spines]

Nodonchus cf. ***bambusifer*** White 1961 Figs 31, 32

MATERIAL. Three spines; P62871, P62859 from samples 8, 9 in the Jauf Formation, P62868 from the Wajid Sandstone.

REMARKS. The three spines are dissimilar in shape, but have a similar ornament. The spines have several longitudinal ridges. Their ornament of overlapping ribs and the shallow broad base of insertion of the spines suggest that they belong to the Climatiidae. Together they represent spines from different parts of the body. P62871 is a small fragment from the base of a flattened spine and shows about fifteen ornamented ridges, some of which merge. P62859 is an almost complete spine 41 mm in length, slightly curved, gently convex and tapering rapidly distally. A large part of the insertion area is present, and is set at an angle of 35° to the axis of the spine. P62868 is 21mm in length, stout and rapidly tapering, and may be a spine from an intermediate series. P62859 and P62868 both show a broad base of insertion. The ornament ridges remain separate from one another and taper to match the overall tapering of the spine. The ornament is of truncated nodes developed symmetrically along the axis of each ridge (cf. the asymmetrical nodes of *Climatius latispinus*) although each truncation is set at a shallow angle. The pattern and spacing of ornament is similar to that of *N. bambusifer* White 1961 (Lower Siegenian, Shropshire, England), the difference being that the spines from Saudi Arabia are more flattened.

Subclass **CHONDRICHTHYES**
Infraclass **ELASMOBRANCHII**

Genus *ANTARCTILAMNA* Young 1982

Antarctilamna sp. Figs 29, 30

Three specimens (P62817a, b, P62818 and P62819a, b) from the Wajid Sandstone consist of groups of scattered, small compound scales preserved as impressions. No histological details are preserved but sufficient surface topology remains to suggest that they belong to *Antarctilamna* and that these scales may be associated with *Antarctilamna*-like spines also found in the Wajid Sandstone. Each scale is ovoid to circular, about 2 mm in the greatest diameter, and since they are all about the same size on each of the scatters they probably each represent single portions of the squamation. The crown of each scale is rather flat and the base is much smaller, located at the anterior end and is connected to the crown through a neck. This is typical of some Silurian and Devonian elasmobranch scales (*Cladolepis* Wells 1944, Gross 1973; *Maplemillia* Gross 1973; *Elegestolepis* Karatajute Talimaa 1973; *Ellesmereia* Vieth 1980; *Antarctilamna* Young 1982). Other elasmobranch scales show a base and crown of roughly equal size. The Wajid scales, like those of *Cladolepis* and *Antarctilamna* show a surface ornament of long ridges which tend to follow the margin of the crown, together with an area anteriorly which is covered with small, partially recumbent, grooved spines. These scales are uniquely like *Antarctilamna* in having an open cup-shaped base.

Antarctilamna prisca Young is known from late Givetian/ early Frasnian of south Victoria Land and New South Wales. Gagnier *et al.* (1988) described a second species, *A. seriponensis* from the Emsian of Bolivia. *Antarctilamna* probably also occurs in the Eifelian of Iran (see Young 1989: 50) because the spine illustrated by Blieck *et al.* (1980: pl. 1, fig. 20) and described as having *Ctenacanthus* type ornament is indistinguishable from *Antarctilamna*.

Four specimens of fin spines may belong to *Antarctilamna*. P62820, P62822, P62823 and P62821 are all short, stout spines. P62821 (Fig. 29) is by far the best preserved, measuring about 25 mm long and being 15 mm broad at the base. These proportions are similar to the larger spines of *Antarctilamna* figured by Young (1982: pl. 87). The spines are nearly straight with a narrow zone of insertion. They are marked with prominent costae which are composed of cone in cone ornament. In this they resemble ctenacanth spines but, as Young (1982) pointed out, this type of ornament may have been the primitive elasmobranch type found in both ctenacanths and xenacanths. In P62821 there are about eight costae on either side of the midline. P62822 and P62823 represent parts of larger spines in which there are approximately 13 costae on either side, a number more like that found in *Antarctilamna prisca* Young. The number of costae may simply reflect size.

Family **PHOEBODONTIDAE** Williams 1979

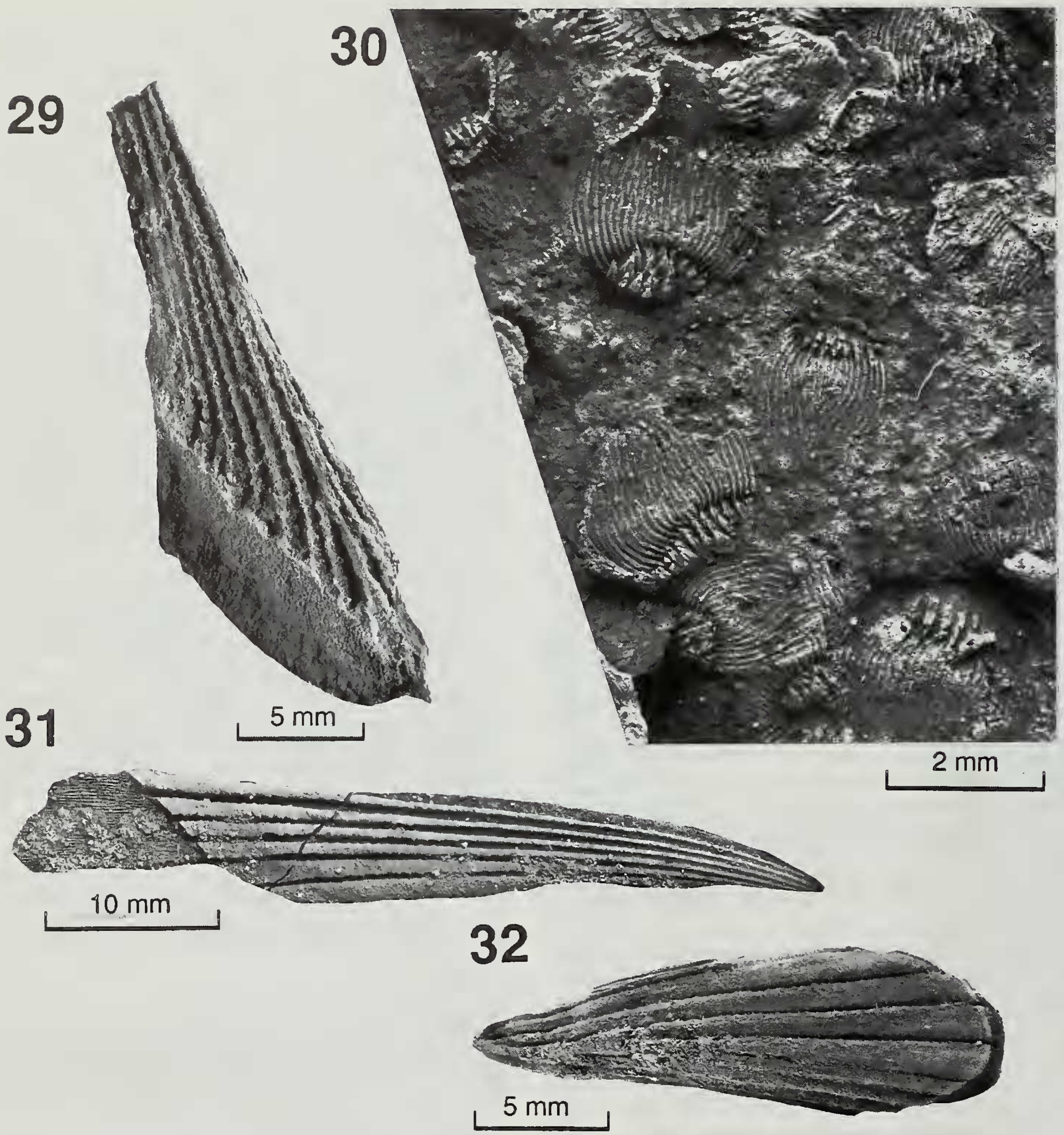
Genus *PHOEBODUS* St John & Worthen 1875

Phoebodus sp. Fig. 7

A single tooth (P62874) in sample 22 from the Jauf Formation represents a diplodont tooth and although broken, enough remains to allow determination as a tooth of *Phoebodus*. The base is tumid, pierced by four relatively large nutritive foramina (cf. *Antarctilamna* where the base is pierced by many formina, Young 1982: fig. 3). The crown has two lateral and slightly divergent cusps with three inner cusps. Unlike named species the inner cusps tend to be rather small. An isolated cusp on the same specimen shows faint striations and such were mentioned for the type species *P. sophiae* by St John & Worthen (1875). *Phoebodus* species are known from the Middle Devonian to Upper Carboniferous of North America, although it is highly likely that some of the younger forms should more properly be referred to other genera.

Form genus '*CLADODUS*' Agassiz 1843

There are many teeth present in sample 9 (preserved on specimens P62855 and P62856) which can only be referred to the form genus *Cladodus*. These are Palaeozoic shark teeth



Figs 29–30 *Antarctilamna* sp. 29, spine P62821 (cast). 30, group of scales P62819a (cast).
Figs 31–32 *Nodonchus* cf. *bambusifer* White. 31, median spine P62859 (cast). 32, intermediate spine P62868 (cast).

with a long central cusp and two or three much smaller lateral cusps. They are known from the Lower Devonian onwards. In the Saudi Arabian sample these teeth are rolled and worn such that usually only the central cusp remains on the swollen root. The central cusp may reach 8 mm in length. The lingual surface of the cusp is striated at the base.

ACTINOPTERYGII

Rare actinopterygian scales have been found in samples 15 and 26, Jauf Formation. They are rectangular in outline and show a convex base. The outer surface is marked by a prominent diagonal ridge passing anterodorsally–posteroventrally. There are a few minor ridges which follow the principal ridge.

DISCUSSION

The discussion which follows deals briefly with comparisons between the Saudi Arabian fish fauna described here and some other fish faunas of the Devonian. Despite being

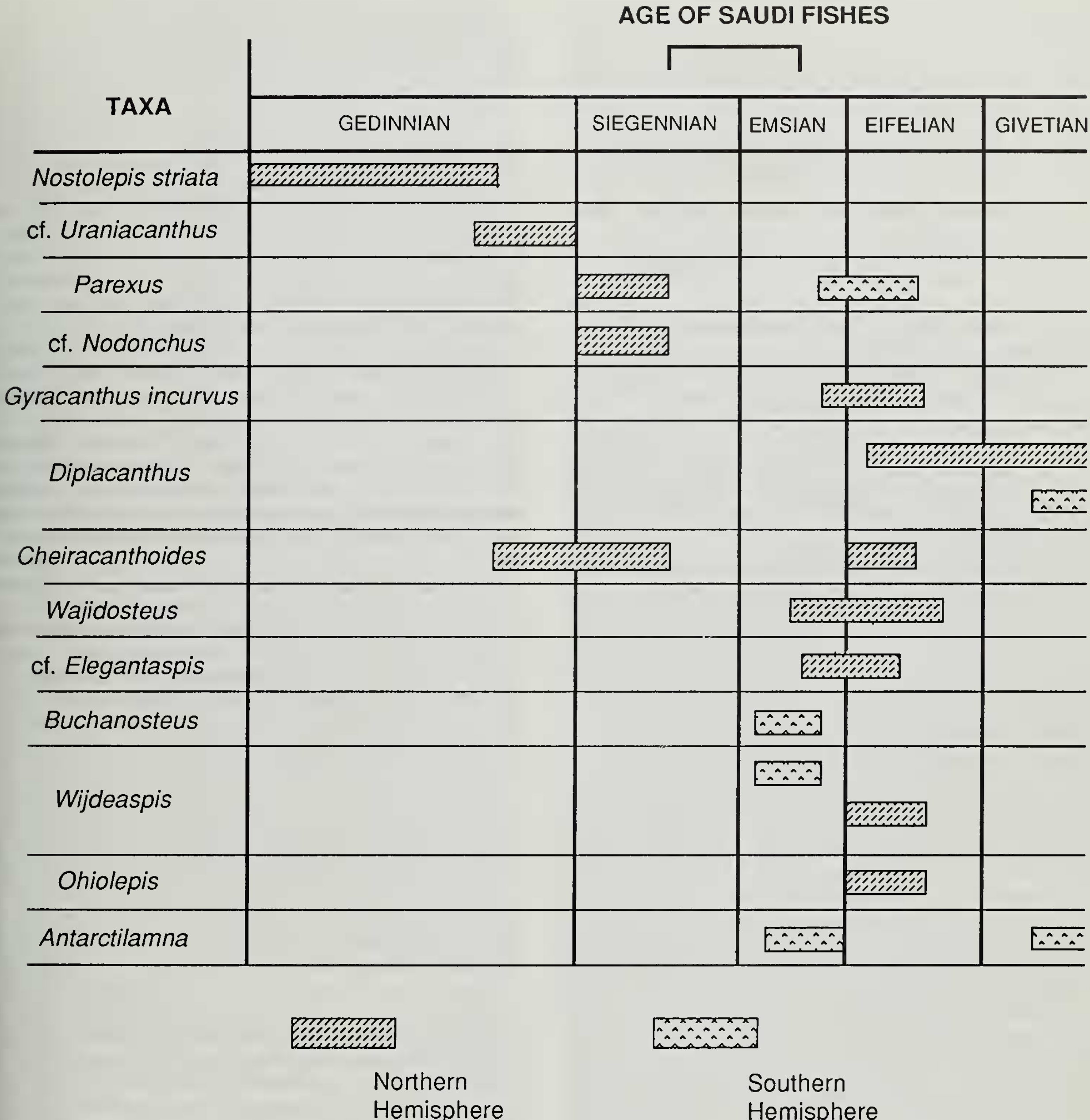


Fig. 33 Chart comparing the stratigraphical distribution of some of the taxa found in the Saudi Arabian fauna with comparable taxa elsewhere in the world.

represented by fragmentary material, the present fauna adds to our knowledge of Devonian fishes from the Middle East. Its significance may only be assessed within the context of biostratigraphical and biogeographic comparisons. Boucot *et al.* (1989) estimated the age of the Jauf Formation invertebrate fauna as Pragian–Early Emsian and the fishes do not contradict this determination, which is therefore accepted here.

Figure 33 shows the stratigraphic distribution of the Saudi Arabian fish taxa, or near relatives, plotted against those same taxa occurring in other parts of the world. Because Saudi Arabia lay near the equator in Lower Devonian times (Scotese & McKerrow 1990), it is pertinent to show comparisons with reference to both northern and southern hemisphere fish occurrences. Fish faunas of exactly the same age are very rare, although they may be represented in Spitzbergen (Wood Bay Series) and perhaps Canada (Battery Point Formation and Atholville Beds). For those taxa found both in Saudi Arabia and in northern hemisphere faunas, then, the match is either with contemporaneous taxa (cf. *Elegantaspis*, *Gyracanthus incurvus*) or with taxa which are older than in Saudi Arabia (*Uraniacanthus*, *Parexus*, *Nodonchus*). For those shared between Saudi Arabia and the southern hemisphere the match is either with contemporaneous taxa (*Buchanosteus*, *Wijdeaspis*) or younger (diplacanthid, *Antarctilamna*). This raises an interesting question, since Saudi Arabia was firmly part of Gondwana in Lower Devonian times and was supposedly separated from northern landmasses such as Laurentia, Baltica, and Angaraland by a Rheic ocean (Scotese & McKerrow 1990). It might therefore be expected that taxa which are represented in deposits which are older elsewhere would have southern hemisphere affinities. In fact it is quite the reverse (also see below).

Leaving this point aside temporarily, the total aspect of the Saudi Arabian fish fauna is recognized as 'Gondwanan' as characterized by Young (1987). For instance, the Saudi Arabian fauna consists only of acanthodians, placoderms and sharks (with a few actinopterygian scales). There are no heterostracans, osteostracans or galeaspids. This negative evidence, of course, might be explained by the fact that Saudi Arabia lies outside any of the Provinces containing these taxa (Young 1981). With a few exceptions, the absence of these taxa in Lower Devonian deposits is typical of Gondwanan faunas. The absence of thelodonts cannot be explained on straight geographic grounds because Saudi Arabia should lie well within the *Turinia* province (Turner & Tarling 1982). The absence of thelodonts may be a facies problem. There are also no actinolepid placoderms. Their rarity is an acknowledged feature of Lower Devonian Gondwanan faunas (Young 1987). On the positive side, the presence of *Antarctilamna* ties it to Gondwana since this is found in younger deposits of Antarctica and Australia, but it is also found in roughly contemporaneous deposits of Bolivia, South America (indet. chondrichthyan, Gagnier *et al.* 1989*b*: *Antarctilamna seriponensis* Gagnier *et al.* 1988). As far as we know, *Antarctilamna* is exclusively southern hemisphere. The evidence from structural geology and palaeomagnetism suggests that Arabia was part of northern Gondwana, probably lying 15°–30° south of the Lower Devonian equator (Scotese & McKerrow 1990). But does the fauna agree entirely with our concepts of Gondwanan fish faunas and how does it relate to other fish faunas? Figure 33 shows that there are more associations with taxa in the northern hemisphere. This may reflect true historical pattern or bias in collecting and description. The acanthodians, in particular, appear to have closer affinities with those in the northern hemisphere. Most of these are climatiids which are generally rare in the southern hemisphere. Exceptions may be some climatiid remains from the Lower Devonian (?Gedinnian) described from Brazil (Janvier & Melo 1988). *Nostolepis* scales are found in S. China (Gagnier *et al.* 1989*a*). So it is possible that climatiids and perhaps ischnacanthids were worldwide at the beginning of the Devonian. Amongst the climatiids there is a particular similarity with *Gyracanthus incurvus* of eastern Canada. On the other hand one of the diplacanthid acanthodians is closely similar to the un-named diplacanthid from Antarctica. Amongst the placoderms, then, the similarity of *Wajidosteus* and *Elegantaspis* with phlyctaeniids from eastern Canada and Spitzbergen is important. But the other placoderms tell a different story. *Buchanosteus* is an Australian form, although we know of close relatives in S. China and in Iran (Goujet & Janvier 1989), perhaps also in Kazahkstan (Lelièvre 1989). The petalichthyid *Wijdeaspis* is known from Australia, but is also found in Spitzbergen and, in slightly younger rocks, in Siberia. Petalichthyids, like climatiids, may well have been world wide in the early Devonian. Finally, *Antarctilamna* is elsewhere found in the southern hemisphere, although it needs pointing out that the Saudi collection does contain scales resembling *Ohiolepis* which are elsewhere found in the northern hemisphere, as are the teeth *Phoebodus* and *Cladodus*.

This rather intermediate position of the Saudi Arabian fauna, with elements traditionally regarded as both of northern and of southern hemisphere origin, requires some explanation. The first question we may ask is: is this fauna unique? If so it may just be a quirk of sampling. Faunas which are geographically and stratigraphically nearby include those from localities in North Africa and Iran. The area immediately adjacent to Saudi Arabia is Iran even though most of Iran was located on a different plate closely adjacent to the Arabian shield (Scotese & McKerrow 1990: fig. 14). The northern Iranian fish locality of Khush Yeilagh is usually regarded as slightly younger than the Saudi locality, being early Eifelian in age, although some work by Hamdi & Janvier (1981) on the condonts of the beds overlying the fish-bearing parts of the Khush Yeilagh Formation suggests an Emsian age. The Iranian fauna has been described by Blieck *et al.* (1980). It is far more diverse than that of Saudi Arabia but there are some common elements. Buchanosteids are present in both, as are elasmobranch spines resembling *Antarctilamna* (Blieck *et al.* 1980: pl. 1, fig. 20) and there is a very similar *Gyracanthus* spine (1980: fig. 7C, D). The Iranian fauna also includes small phlyctaeniids, although none appear conspecific with those from Saudi. The Iranian fauna is usually compared with those of Gondwana and China. *Antarctilamna* is certainly Gondwanan. Buchanosteids are shared with both eastern Australia and China which may be considered closely tied to Gondwana. But it is worth noting that buchanosteids may also be present in Kazakhstan (Lelièvre 1989), a truly northern locality. Janvier (*in* Blieck *et al.* 1980) identified some trunk plates of an antiarch from Iran as being closely similar to a form from the Middle Devonian of south China (*Hyrcanaspis* Janvier & P'an 1982). Many other elements of the Iranian fauna are not obviously Gondwanan and have affinities elsewhere. Goujet (*in* Blieck *et al.* 1980) thought that the small phlyctaeniids were like those of the Emsian–Eifelian of Quebec. Mark-Kurik thought that the holonematids were like those of the Baltic. Goujet thought that the coccosteids were similar to those of Scotland and that the groenlandaspids were more like those of Germany than of Australia. Janvier thought that the acanthodians and the sarcopterygians were similar to those of Germany as well as the Baltic and North America (all *in* Blieck *et al.* 1980). There is therefore a similar pattern to the fauna from Saudi Arabia. Both have a Gondwanan (and south China) element but it is nevertheless overshadowed by animals more similar to those occuring in northern areas.

From Morocco, Lelièvre (1984, 1988) has described Emsian arthrodires *Atlantidosteus* and *Antinosteus* which can be demonstrated to have sister taxa in the Emsian of eastern Australia. But there is nothing in common between Saudi Arabia and Morocco. Other localities which may be of significance are found in northern Spain and Rhenish Bohemia, associated with remnants of plates dubbed as Armorica. Armorica has always been problematical, even to details of recognizing what constitutes Armorica (see Young 1987:286), but most workers recognize that Armorica began its history as part of Gondwana (Cocks & Fortey 1982). There are very few taxa shared between the Lower Devonian of Spain and Saudi Arabia or Iran. The Spanish localities have been described by Mader (1986) and most of the taxa there have northern affinities, including the presence of heterostracans. It has to be said that the Spanish localities are predominantly Gedinnian in age, much earlier than the Saudi Arabian or Iranian faunas. The other localities, of which there are a great number, are found in the Pragian and Emsian Hunsrück-schiefer. There is a large fauna here (Gross 1951) and it contains typically northern fishes such as cephalaspids and heterostracans, as well as placoderms such as *Gemuendina* and *Lunaspis* which are closely related to forms in South America and eastern Australia respectively, with *Lunaspis* being additionally found in China (Liu 1981). It also contains *Speonosydrion*, a dipnoan originally described from the Emsian of eastern Australia. The fish faunas of Rhenish Bohemian localities show some similarity with the fauna from Saudi Arabia and Iran. There are similar placoderm scales. The tiarapsid-like groenlandaspids and some acanthodian spines of Iran suggest Rhenish Bohemian affinity (Blieck *et al.* 1980). With the invertebrate evidence from Saudi Arabia (Boucot *et al.* 1989), such as one trilobite species which is only found elsewhere in Rhenish Bohemia and two brachiopod species known from northern Spain, this may be confirmation that the Lower Devonian Saudi Arabian fauna belongs with that of northern Iran and with the Rhenish Bohemian faunal province. How the Rhenish Bohemian endemism was established is more problematical. To consider it as Gondwanan may be over-simplified (see also Young 1990:247) because this is a huge area spread over a large part of the southern hemisphere. The faunas of eastern Gondwana (eastern Australia and part of Antarctica) contain fishes (e.g. wuttagoonaspids) sufficiently distinct to justify characterizing an East Gondwana province (Young 1981) which, in turn, may have closer connections with south China than anywhere else. On the other side of Gondwana, the newly described Devonian fish faunas of Bolivia (Gagnier *et al.* 1988) and Brazil (Janvier & Melo 1988) show similarity, albeit not a unique similarity, with North America and the Rhenish Bohemian province (rhenanids, *Machaeracanthus*). With such limited amounts of information detailed conclusions about more distant associations cannot be justified. Without cladograms and theories of sister-group relationships there is little chance of being able to tie two areas together to the exclusion of others.

With the present state of knowledge we can say that the Saudi Arabian fauna probably belonged within the Rhenish Bohemian area of endemism in the late Pragian/early Emsian and no doubt this area of endemism was independent from the Euramerican basin as described by Blieck (1982). But there are some elements of the Saudi Arabian fauna chiefly the phlyctaeniids, petalichthyids and some of the climatiids which suggest an earlier connection with more northern areas, perhaps before a vicariance event created the Euramerican and Rhenish Bohemian faunal realms.

We conclude that the Lower Devonian fish fauna from Saudi Arabia discussed here belongs with that of the Rhenish–Bohemian Province, but that there are affinities with older faunas in the northern hemisphere and younger faunas in the southern hemisphere.

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APPENDIX

List of sample numbers with brief lithological description and fauna. Samples presented in stratigraphical order (see Fig. 2). Sample numbers are the original numbers given in the field. Geographical localities are indicated in Fig. 1.

Sample 3 29°49·7′N 39°50·4′E, Jal al Gharb, Jauf Formation, Shai'ba Member, about 30 m below top. Light grey-green, grey, and maroon, fissile, partly silty shale with a few grey-tan, fine crystalline dolomite streaks, and common small phosphate grains and very small rolled bone fragments. Petalichthyid P62862, P62863a, b; *Wajidosteus* P62865; ischnacanthid tooth whorls P62866, P62867; *Nostolepis striata* scales. Probable depositional environment: quiet brackish water in mud lagoons.

Sample 9 29°27′N 38°27′E, Ja'alat as Sawada, Jauf Formation, Sha'iba Member, about 6 m above base. Hard, red, fine-grained, black-weathering ferruginous sandstone. *Gomphonchus* symphysial tooth whorl P62853; *Cladodus* P62854–6; indet. climatiid spines; *Nodonchus bambusifer* P62859; *Uraniacanthus spinosus* P62860, P62861; climatiid indet. spine P62857, P62858; *Nostolepis striata* scales. Probable depositional environment: flood plain or fluvial channel outwash, deposited in minor sea level lowering event during Shai'ba times. Red colour suggests penecontemporaneous oxidation.

Sample 8 29°27′N 38°27′E, Ja'alat as Sawada, Jauf Formation, Sha'iba Member, about 32 m above base. Yellow to light red, very hard, fine grained sandstone with thin, silicified lenses just below top. Conchostracans; *Rhabdostichus* sp.; eurypterids cf. *Willwerathia* or *Rhenopterus*; a single lingulid; *Parexus* P62870; *Nodonchus bambusifer* spines P62868, P62871; *Wajidosteus* P62869. Probable depositional environment: presence of conchostracans lends support to a non-marine aspect (the one lingulid may be due to backwash or reworking from a near shore marine environment); the yellow and light red colours suggest penecontemporaneous oxidation due to subaerial exposure.

Sample 11 29°28′N 39°34′E, near Barqa As-Sha'ira, approx. 47 km southwest of Al Jawf, about middle of Subbat Member. Yellow, partly porous and hard, calcarenitic, very fossiliferous limestone/dolomite stringer. Apparently not present in type section area. Petalichthyids P62949 and P62950; corals, bryozoa, brachiopods and bivalves. Probable depositional environment: shallow water marine environment.

Sample 7 29°55′N 39°48·5′E, Ajrabah, Jauf Formation, Subbat Member, about 47 m below top. Grey and grey-tan, argillaceous and calcareous siltstone and grey silty shale. Lingulids very common; eurypterid impressions; *Onchus* spines P62873 and P62872. Probable depositional environment: quiet brackish water in mud lagoons.

Sample 24 29°55′N 39°48·5′E, Ajrabah, Jauf Formation, Subbat Member about 32 m below top. Light golden yellow, soft fine grained sandstone stringers in shale. *Jaufolepis striata* gen. et sp. nov. (P62957a, b). Probable depositional environment: fluvial outwash during minor sea lowering event.

Sample 25 29°51′N 39°52·7′E, near Al Jawf Gardens, Hammamiyat Member, 2–3 m above top of first Hammamiyat limestone. A thin grey-tan, hard, dense, limestone/dolomite stringer. Many fish fragments representing unidentifiable phylctaeniid arthrodires; *Buchanosteus*; brachiopods, corals, bivalves, bryozoa and ostracods. Probable depositional environment: shallow water marine environment.

Sample 26 29°50·8′N 39°52·6′E, Subbat el Wadi, Jauf Formation, base of Transition Zone Member. Yellow soft, friable, medium grained sandstone, with rip up clasts of underlying grey clay. *Nostolepis striata* scales (P62952), actinopterygian scales, diplacanthid scales (P62951). Probable depositional environment: fluvial channel or channel outwash.

Sample 15 30°01·7′N 39°58·2′E, Tell al Murair, Jauf Formation, top of Transition Zone Member. Soft sandstone, fine grained, micaceous, with red siltstone streaks and rip up clasts of underlying channeled grey clay. *Nostolepis striata* scales (P62954), *Cheiracanthoides* scales (P62953), actinopterygian scales, diplacanthid scales, actinolepid trunk plates. Probable depositional environment: shallow, possibly braided, fluvial channel.

Sample 17 30°4′N 40°5′E, Qiyal Sagiyr, Jubah Sandstone, about 40 m above top of Jauf Formation. Red siltstone and fine grained, soft and friable, white speckled sandstone. Many broken and rolled fish scales and plates, all difficult to identify. Some plates have ornament reminiscent of *Buchanosteus* (approximately regular tubercles, stellate at the base) but this type of ornament is by no means restricted to this genus. Scales include those of placoderms (P62958–60) and those of *Nostolepis striata* (P62956). Probable depositional environment: high energy fluvial channel outwash or flood plain; red colour suggests penecontemporaneous oxidation due to subaerial exposure.

Sample 22 30°13·6′N 40°09·2′E, Adhiriyah, Jubah Sandstone, about 110 m above top of Jauf Formation. Very hard, tan, fine grained sandstone capping yellow shale, with small pockets of softer, red, fine grained sandstone with phosphate pellets and rolled fish remains. One lingulid brachiopod; broken acanthodian spines; diplacanthid scales, a scale of *Cheiracanthoides* sp. (P62955); *Phoebodus* sp. (P62874). Probable depositional environment: high energy fluvial channel outwash or a flood plain (the one lingulid may be due to backwash from a nearby shallow-water marine shore environment).

Wajid Sandstone 17°36′N 44°5·5′E. Fine, very silty and well indurated, varicolored micaceous claystone. *Gyracanthus incurvus* (P62810, P62811, P62812, P62813a, b, P62814a, b, P62815a, b, P62816a, b); *Antarctilamna* (P62817a, b, P62818, P62819a, b, P62820, P62822, P62823, P62821, P62824, P62825); *Wajidosteus minutus* (P62826, P62827, P62828, P62829, P62830, P62831, P62832, P62833a, b, P62834a, b, P62835a, b, P62836a, b); cf. *Elegantaspis* (P62837); petalichthyid (P62838); phlyctaeniids (P62839, P62840, P62841, P62842, P62843, P62844, P62845a, b, P62846a, b, P62847a, P62848); actinolepid (P62849a, b); *Nodonchus bambusifer* spine (P62868). Probable depositional environment: very quiet water in restricted basin, possibly a cut-off lagoon.

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